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Originals

Morphology and Variation of Cleistogamous Flowers in *Lespedeza tomentosa* (Thunb.) Siebold ex Maxim. (Leguminosae) in Relation to Variation in Inflorescence Form

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Morphological variation of cleistogamous (CL) flowers were examined in *Lespedeza tomentosa* (Thunb.) Siebold ex Maxim. The CL flowers always have five petals although their size is reduced, and they vary in numbers of stamens and pollen sacs due to reduction. The numbers of stamens per flower and pollen sacs per anther vary from ten to six and from four to zero, respectively. The inner whorl (antepetalous) stamens tend to be reduced more conspicuously than the outer whorl (antesepalous) ones and the abaxial stamens than the adaxial ones within the same whorl in the CL flower. The two antesepalous stamens located on the most adaxial position are always retained and produce fertile pollen sacs in CL flowers. The position of these stamens is closely related to self-pollination, because the stigma comes to contact with them by the adaxially curved style. Moreover, degree of such reduction in the CL flower is closely related to the form of inflorescence to which the flower is attributed and to the position within the inflorescence.

The genus *Lespedeza* is attributed to the subtribe Lespedezineae of the tribe Desmodieae in Leguminosae, and it comprises about 40 species (Ohashi et al. 1981). Under this genus two infrageneric taxa, Lespedeza and Macrolespedeza treated as sections (Schindler 1913, Akiyama 1988) or subgenera (Ohashi 1982), have been recognized mainly on the basis of the presence or absence of cleistogamous (CL) flowers. The subgenus Lespedeza has CL flowers and is distributed in Asia and North America, while the subgenus Macrolespedeza produces no CL flowers and is distributed in Asia.

The CL flowers are generally defined as flowers never achieve anthesis but produce fruits by self-pollination. The cleistogamy – the production of CL flowers – is widespread in the angiosperms. Lord (1981) counted 56 families 287 species, and classified types of cleistogamy into four categories based on the ability of anthesis, the productivity of chasmogamous (CH) flowers, and the degree of morphological differences of CL flowers from CH flowers. She cited twelve species of *Lespedeza* as with dimorphic (CH and CL) flowers on an individual based on previous references and as being attributed to one of her categories "true cleistogamy". CL flowers of *Lespedeza*, moreover, have been described as being apetalous (Torrey and Gray 1840; Maximowicz 1873; Schindler 1913; Nakai 1927; Fernald 1950) or unisexual (Torrey and Gray 1840). According to Blake (1924), all gradations exist between the nearly or quite apetalous flowers, with stamens greatly reduced or perhaps sometimes entirely wanting, and the petaliferous flowers in some American species, while the reduction is not so greatly in others. Nakai (1927) described petals and stamens as being reduced entirely or having their remnants in CL flowers of Japanese and Korean species. Hanson and Cope (1955), on the other hand, described CL flowers in ten species of *Lespedeza* as having five petals, which are somewhat shorter than the calyx, and ten anthers.

Although the presence of CL flowers is one of the most important characteristics of subgenus Lespedeza, their morphological features are still uncertain. The present study was therefore intended to clarify the morphology and variation of CL flowers in *Lespedeza* by observing and examining *L. tomentosa* (Thunb.)[1] Siebold ex Maxim. Because this species produce much more flowers within an inflorescence than other species, we considered this species to be the most convenient material for the investigation of morphological variation of CL flowers within and between inflorescences.

Materials and Methods

Materials were collected from the following three localities in northern Honshu of Japan: Iwate Pref., Takizawa-mura (cultivated in the Experimental Garden of Biological Institute, Tohoku University; no voneher, 19 Aug. 1982; this material called *Takizawa* in the present paper); Yamagata Pref., Higashine-shi (T. Nemoto 1392, 30 Aug. 1982); Miyagi Pref., Nakaniida-cho (T. Nemoto 9008301, 30 Aug. 1990). Inflorescences of these materials were fixed with FAA. Voucher specimens were retained in TUS.

For observation of the variation of flower morphology, we particularly noticed the numbers of stamens and pollen sacs as an indicator of the degree of development of the CL flower. Inflorescences bearing fully developed flowers and/or fruits in young stage were chosen for observation. We regarded the CL flower with a collapsed stigma as being fully developed, because the stigma becomes collapsed after its contact with anthers for self-pollination as shown later. From our preliminary observations, moreover, we found that the stamens and anthers are persistent in CL flowers even after pollination, and therefore we could use flowers at the stage of young fruit. In contrast, the anthers of CH flower, which contain four pollen sacs, usually fall away from their filaments after flowering. Within an inflorescence flowers are arranged in pair at each node of the axis in *L. tomentosa* as is common in the genus (cf. Nemoto and Ohashi 1990). One of the paired flowers was arbitrarily selected for observation in almost all inflorescences examined.

To investigate its morphology FAA-fixed flowers were dissected under a binocular microscope. For observation by scanning electron microscope, FAA-fixed flowers were dehydrated through an ethyl alcohol series, transferred to isoamyl acetate, dried in a critical point dryer, placed on aluminum stubs, coated with gold, and observed and photographed in an Akashi MSM-101 scanning electron microscope.

Results

The CL flower exhibited variation in the degree of development of petals and stamens related to the form of the inflorescence to which they were attributed and to the position in the inflorescence.

General features of inflorescence

The inflorescence is basically borne in the axil of a foliage leaf (Fig. 1A). The foliage leaf is sometimes reduced to the stipules lacking the lamina and the petiole in the distal part of the shoot. The inflorescences subtended by the reduced leaves appear to form a paniculate inflorescence at the distal end of the shoot.

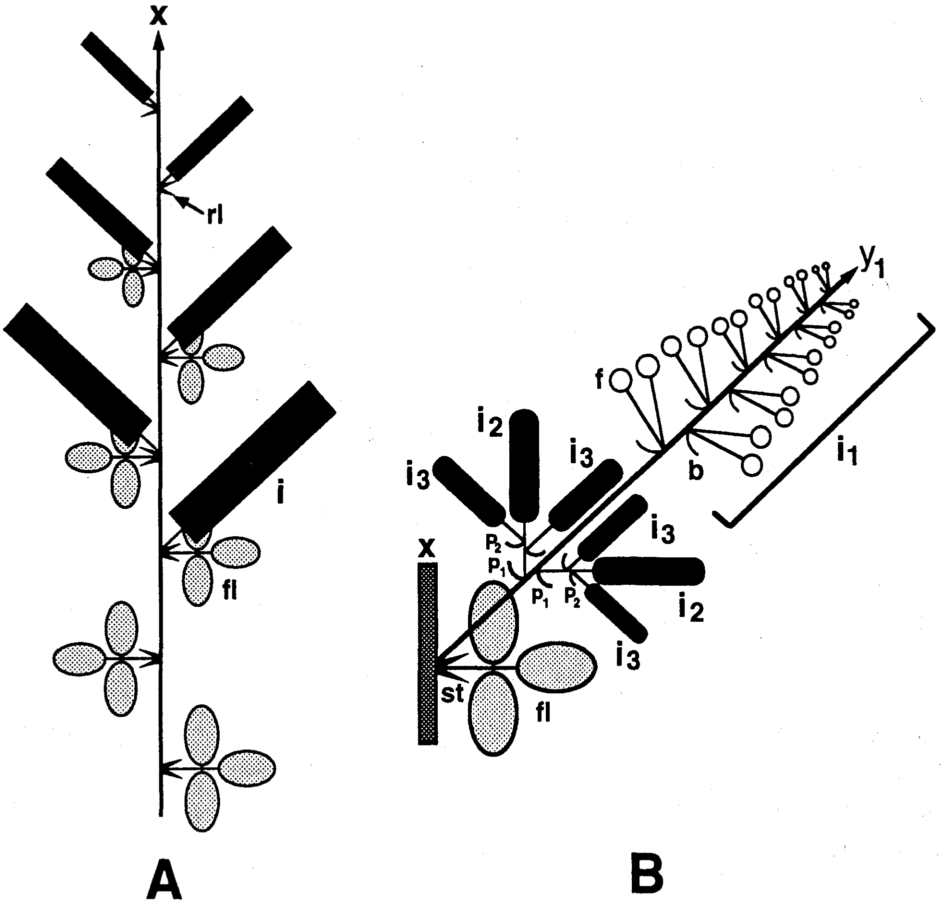

Fig. 1. Diagrammatic illustration of the arrangement of compound inflorescences and flowers in *Lespedeza tomentosa*. A. Arrangement of compound inflorescences on a shoot. B. A compound inflorescence showing first-, second- and third-order partial inflorescences and the arrangement of flowers in the first-order one. b, bract subtending a pair of flowers; f, flower; fl, foliage leaf; i, compound inflorescence subtended by a leaf; i_1, first-order partial inflorescence; i_2, second-order partial inflorescence; i_3, third-order partial inflorescence; p_1, prophyll on first-order inflorescence axis; p_2, prophyll on second-order inflorescence axis; rl, reduced leaf with only stipules; st, stipule; x, axis of shoot laterally producing compound inflorescences; y_1, first-order inflorescence axis.

The inflorescence is a compound pseudoraceme in *L. tomentosa*. The main inflorescence axis arises in the leaf axil (Fig. 1B). At the base of the main inflorescence axis, or first-order inflorescence axis, there are two prophylls, from each axil of which the second-order inflorescence axis arises (i2 in Fig. 1B; Nemoto and Ohashi 1990). The second-order axis has the similar branching system with the main axis, and the third-order inflorescence axis is also formed in each axil of two prophylls at the base of the second-order one.

Flowers are borne in pair in the axil of scale leaves, or bracts, subsequent to the prophylls on the inflorescence axis of each order, which is a characteristics of pseudoraceme (Tucker

1987). Here we call the clusters of flower pairs on first-, second-, and third-order inflorescence axes in an inflorescence first-, second-, and third-order partial inflorescences, respectively. In the present study, we examined first- and second-order partial inflorescences in detail.

Variation in inflorescence form and its relationship with the relative productivity of CH and CL flowers

There was conspicuous variation in the length of the first-order inflorescence axis and in the relative productivity of CH and CL flowers on the axis (Fig. 2). The first-order partial inflorescence, therefore, varies in form from pedunculate and slender (Fig. 2A) to sessile and condensed (Fig. 2F). The degree of elongation of the first-order inflorescence axis was closely related to the relative productivity of CH and CL flowers, that is, the first-order partial inflorescence producing more or less CH flowers has longer axis than that producing only CL flowers. When both CH and CL flowers were produced in the same partial inflorescence, moreover, there were three patterns of flower arrangement along the first-order inflorescence axis from proximal to distal end: CH flowers to CL ones (Fig. 2B), CL to CH (Fig. 2C), and CL to CH then to CL ones (Fig. 2D). On the other hand, second- and third-order partial inflorescences commonly had axes extremely shortened in length and were composed of only CL flowers.

Based on the relative productivity and arrangement pattern of CH and CL flowers in the first-order partial inflorescence and the length of the first-order inflorescence axis and the internodes, we distinguished the inflorescence forms into the following three types and five subtypes (Fig. 2) in order to examine the morphological variation of CL flowers in relation to the inflorescence form.

Type I: The first-order partial inflorescence is composed of only CH flowers (Fig. 2A). It usually has the most elongated axis and peduncle.

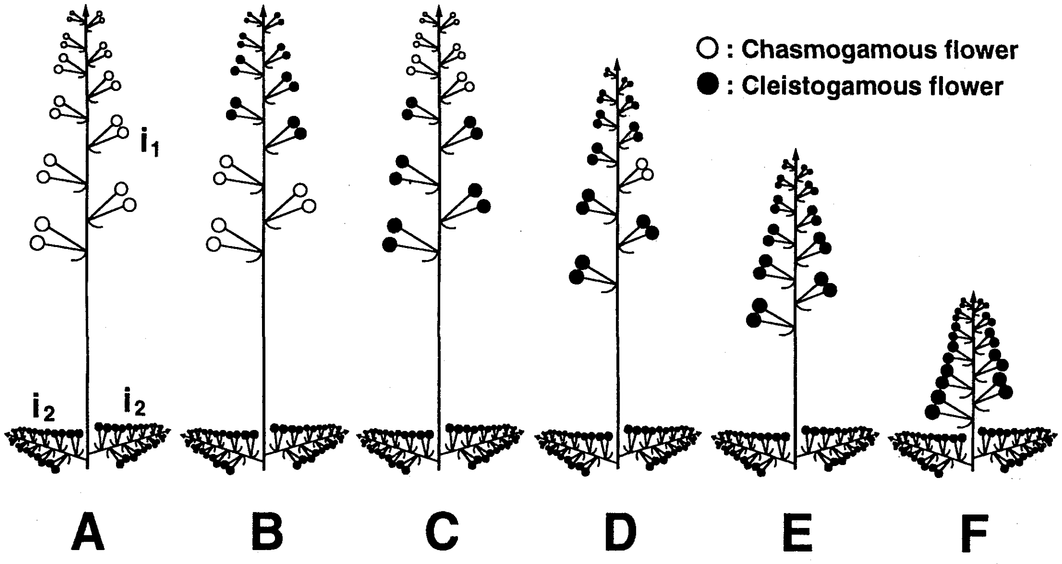

Fig. 2. Inflorescence types distinguished by the arrangement pattern of CH and CL flowers and the length of first-order inflorescence axis and internodes. A. Type I. B. Type IIA. C. Type IIB. D. Type IIC. E. Type IIIA. F. Type IIIB. i_1, first-order partial inflorescence; i_2, second-order partial inflorescence.

Type II: The first-order partial inflorescence is composed of both CH and CL flowers. It has more elongated axis and peduncle than those of Types III. According to the arrangement pattern of two kinds of flowers along the first-order inflorescence axis from proximal to distal end, three subtypes were distinguished: A) CH flowers to CL ones (Fig. 2B); B) CL to CH (Fig. 2C); C) CL to CH then to CL ones (Fig. 2D).

Type III: The first-order partial inflorescence is composed of only CL flowers. Two subtypes were distinguished on the basis of the degree of the elongation of the inflorescence axis, the internodes and the peduncle: A) the first-order partial inflorescence has longer peduncle and more elongated internodes, and the cluster of flowers is narrowly elliptic to elliptic in shape (Fig. 2E); B) the first-order partial inflorescence is sessile and has extremely shortened internodes, and the cluster of flowers becomes capitate in shape (Fig. 2F).

The material of *Takizawa* included an individual producing inflorescences of only Type IIIB; the material of T. Nemoto 1392 included individuals producing inflorescences of Types IIA and IIIA, B or those of Type IIIA, B; the material of T. Nemoto 9008301 includes individuals producing inflorescences of Types I, IIA–C and IIIA.

General morphology of CL flowers

The CH flower achieves anthesis with exhibiting its conspicuous corolla outside the calyx (Fig. 3A). The CL flower, in contrast, remains closed like flower bud without exhibiting conspicuous corolla (Fig. 3D–J) and, then, the young fruit emerges from the bud-like flower.

The CH flower exhibits a zygomorphic papilionaceous flower which is composed of five sepals, five petals, ten stamens, and a monocarpellary gynoecium (Fig. 3A–C). The five conspicuous petals are twice as long as the calyx (Fig. 3A), two keel-petals of them adhere to each other at the abaxial margin, and two wings adhere to keel-petals at the basal part of the lamina. The ten stamens form a staminal tube by connation and adhesion of their filaments (Fig. 3B). Each of these stamens, moreover, has an dehiscent anther with four pollen sacs.

On the other hand, all CL flowers examined had five reduced petals which are shorter than the calyx (Fig. 3E, H, J). Each petals are separated from each other (Fig. 3H, J), or only two keel-petals are infrequently connate to each other at their abaxial margins (Fig. 3E). The filaments are connate to each other and form a short staminal tube (Fig. 3F, H), or they are free without connation (Fig. 3J). The number of stamens was decreased and varied from ten to six. The anther is indehiscent. The number of pollen sacs per anther was also decreased to three, two, one, or zero. The degree of reduction in the number of stamens per flower and that of pollen sacs per stamen were closely related to the type of the inflorescence to which the flower belongs and to the position of the flower within the inflorescence.

In CL flowers the stigma is positioned adaxially at earlier stages of development of gynoecium (Fig. 4A). As the gynoecium grows, the curved and elongated style gives rise to greater proximity of the stigma to the anthers located on the most adaxial antesepalous stamens (nos. 1 and 2 in Figs. 4B and 5). At this time the surface of the stigma is covered with small papillae. Next the stigma comes in contact with the anthers (Fig. 4C). Although the gynoecium continues to grow after the contact, the surface of the stigma has already been collapsed (Fig. 4D).

Morphological variation of CL flowers

Variation in the numbers of stamens and pollen sacs was investigated in CL flowers from inflorescences of different types. For representing the degree of variation, ten stamens were arbitrarily numbered as shown in

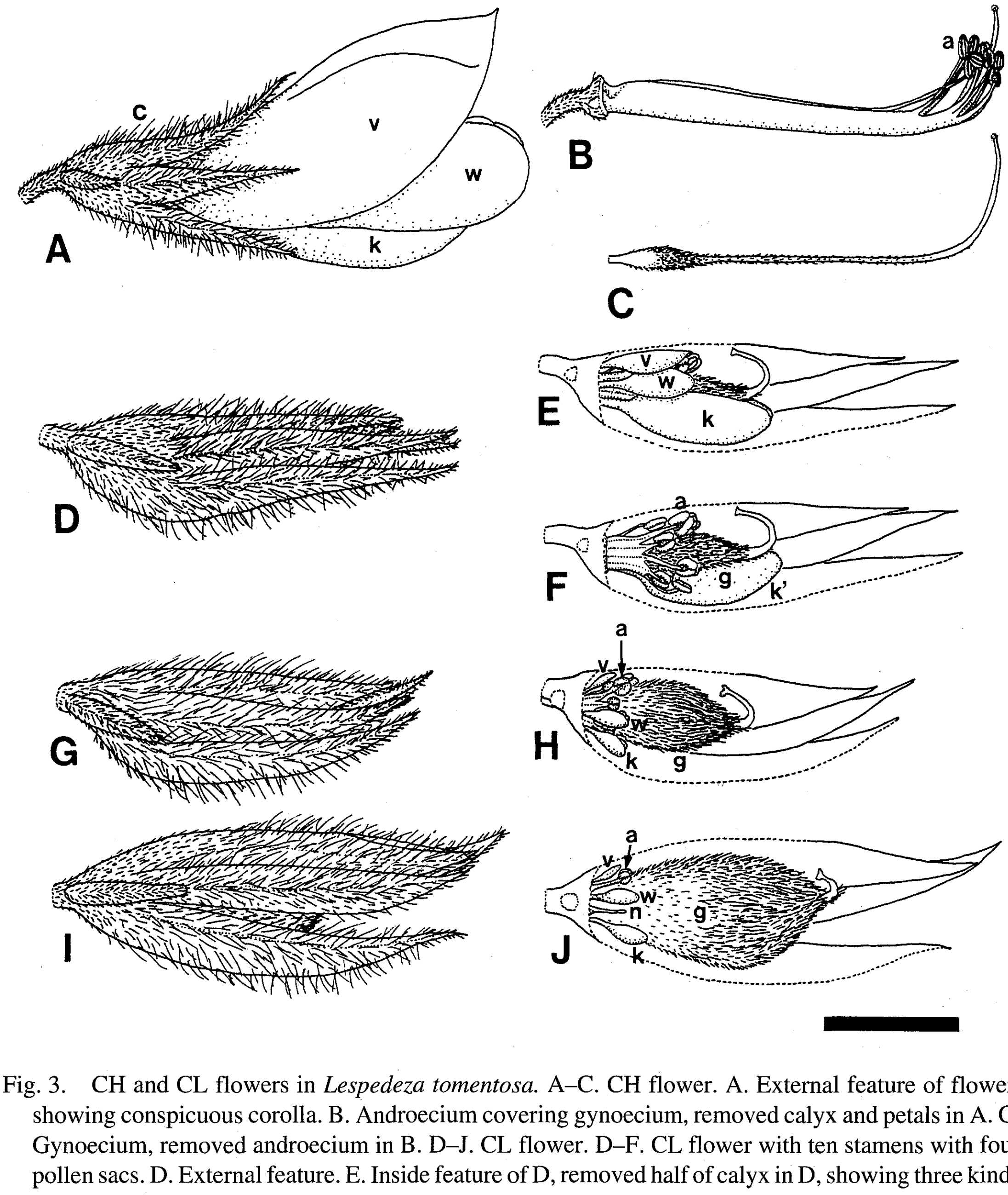

Fig. 3. CH and CL flowers in *Lespedeza tomentosa*. A–C. CH flower. A. External feature of flower, showing conspicuous corolla. B. Androecium covering gynoecium, removed calyx and petals in A. C. Gynoecium, removed androecium in B. D–J. CL flower. D–F. CL flower with ten stamens with four pollen sacs. D. External feature. E. Inside feature of D, removed half of calyx in D, showing three kinds of petals reduced in size but larger than those shown in H and J. F. Inside feature of E, removed standard, wing and keel-petal in E, showing fused filaments and larger anthers including four pollen sacs. G, H. CL flower with ten stamens with anther of two pollen sacs. G. External feature. H. Inside feature of G, removed half of calyx in H, showing three kinds of petals reduced in size and androecium. I, J. CL flower with six stamens only two of them with anther of two pollen sacs. I. External features. J. Inside feature of I, removed half of calyx in I, showing three kinds of petals reduced in size and stamens with anther of two pollen sacs (a) and without it (n). a, anther; c, calyx; g, gynoecium; k, keel-petal at this side; k', keel-petal at that side; n, stamen without anther; v, standard; w, wing. Scale bar = 2 mm (A–C), 1 mm (D–J). (Material: A–H, T. Nemoto 9008301; I & J, *Takizawa*)

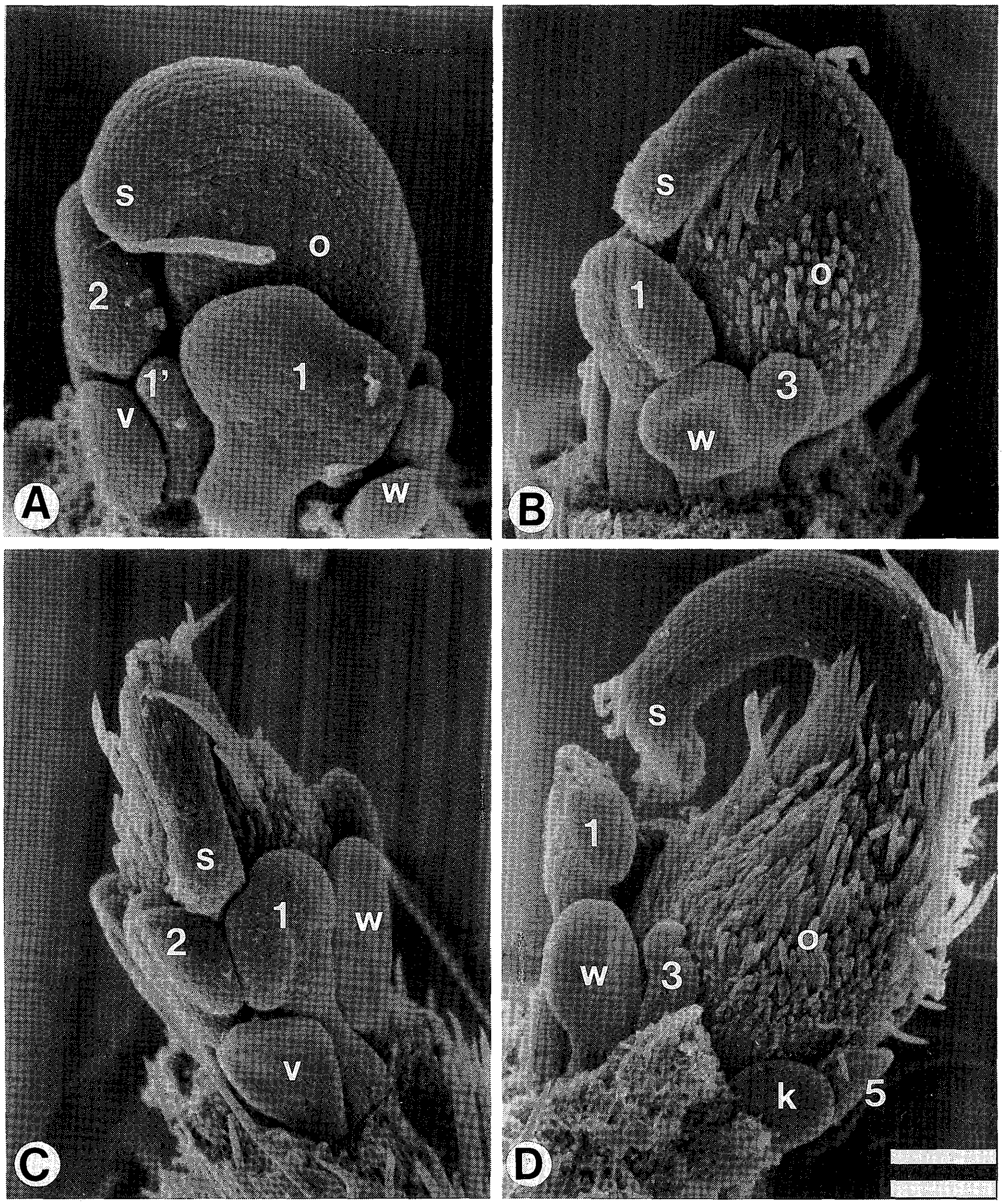

Fig. 4. Relative position of stigma to two most adaxial antesepalous stamens and change in surface view of stigma during developmental processes of CL flower. A, B. Stages before contact of stigma with anthers, showing smooth (A) and small papillate (B) stigmas. C. Stage just being in contact of stigma with anthers. D. Stage after contact of stigma with anthers, showing collapsed stigma. 1, 2, 3, 5, and 1' indicate stamens located on the positions shown in Fig. 5, respectively. k, keel-petal; o, ovary; s, stigma; v, standard; w, wing. Scale bar = 55 μm (A), 100 μm (B–D). (Material: A–D, *Takizawa*)

the floral diagram of Fig. 5. The ten stamens are composed of two five-merous whorls. The five stamens of the outer whorl are placed in front of the sepals, i.e. antesepalous stamens, while those of the inner one placed in front of the petals, i.e. antepetalous stamens. Five antesepalous and five antepetalous stamens were numbered from 1 to 5 and from 1' to 5', respectively.

Inflorescence of Type I (Fig. 6A): An inflorescence was chosen from the material of T. Nemoto 9008301. Flowers of the first-order partial inflorescence were all CH. There were 24 nodes in the first-order partial inflorescence (Fig. 6A-1). In all flower all of ten stamens were normally produced and each of them have four pollen sacs. On the other hands, there were 12 nodes and flowers were all CL in the second-order partial inflorescence (Fig. 6A-2). Although ten stamens were retained in most CL flowers, the number of pollen sacs per anther was reduced to two or one in antesepalous stamens and to one or zero in antepetalous ones.

Inflorescence of Type II (Fig. 6B–D): Inflorescences corresponding to Types IIA, IIB and IIC were chosen from materials of T. Nemoto 1392, T. Nemoto 9008301 and T. Nemoto 9008301, respectively. The numbers of flower-bearing nodes in the first- and second-order partial inflorescences were 20 and 15 in the inflorescence of Type IIA (Fig. 6B), 14 and eight in that of Type IIB (Fig. 6C), and 22 and 11 in that of Type IIC (Fig. 6D), respectively.

CL flowers exhibited variation in the number of stamens and pollen sacs: from flower with ten stamens bearing four pollen sacs (node 4 in Fig. 6B-1) to that with seven stamens four of them bearing two pollen sacs (node 20 in Fig. 6B-1) in the first-order partial inflorescences; from that with ten stamens five of them with two polln sacs, one with one pollen sac and others without pollen sacs (node 1 in Fig. 6C-2) to that with six stamens two of them bearing two pollen sacs, one with one pollen sac and others without pollen sacs (node 14 in Fig. 6B-2) in the second-order partial inflorescences. In all of the inflorescences examined, the closer the CL flowers were to CH ones, the more they had stamens and pollen sacs in the first-order partial inflorescence. Moreover, the ranges of variation in the numbers of stamens and pollen sacs were continuous between CL flowers of the first- and second-order partial inflorescences.

There was difference in the degree of reduction between two whorls of stamens. Although there were five outer antesepalous stamens (1 to 5) in all CL flowers examined, the stamens reduced were all of inner antepetalous ones (2' to 5'). With respect to the number of pollen sacs per stamen, moreover, the latter stamens

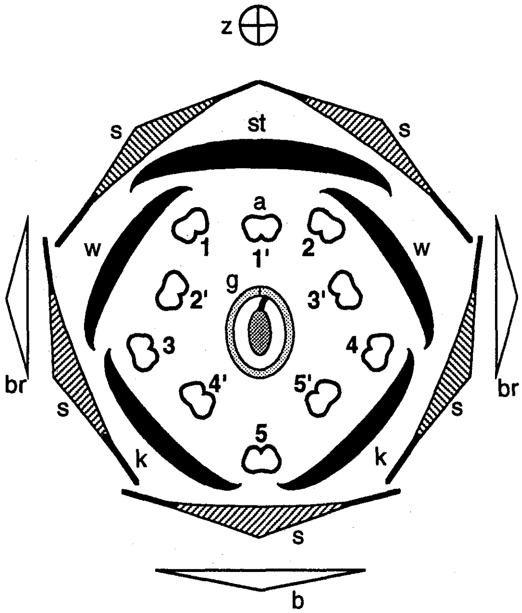

Fig. 5. Floral diagram showing the relative position of outer whorl (antesepalous) stamens (1, 2, 3, 4, 5) and inner whorl (antepetalous) stamens (1', 2', 3', 4', 5'). a, stamen; b, bract subtending each flower; br, bracteole on lateral side of flower; g, gynoecium; k, keel-petal; s, sepal; st, standard; w, wing; z, axis laterally producing flower.

were also heavily reduced than the former ones.

Within the same whorl of stamens, the degree of reduction was different among the positions of stamens. In the outer whorl, stamens of nos. 3, 4, and 5 were reduced the number of pollen sacs more frequently and heavily than those of nos. 1 and 2. Pollen sacs were lost most frequently at the position of no. 5. In the inner whorl, the reduction was more frequent and obvious in nos. 2', 3', 4', and 5' than in no. 1', and it was most conspicuous in the stamens of nos. 4' and 5'. The stamen of no. 1' was never lost, although the pollen sacs were frequently lost.

Inflorescences of Type III (Fig. 6E, F): Inflorescences corresponding to Types IIIA and IIIB were chosen from materials of T. Nemoto 1392 (an individual producing inflorescences of Type III) and *Takizawa*, respectively. First- and second-order partial inflorescences were composed of only CL flowers. The numbers of flower-bearing nodes in the first- and second-order partial inflorescences were 21 and six in the inflorescence of Type IIIA (Fig. 6E) and 17 and 12 in that of Type IIIB (Fig. 6F), respectively.

CL flowers exhibited variation in the number of stamens and pollen sacs: from flower with ten stamens two of them bearing four pollen sacs and eight bearing two (nodes 1, 2, 4, and 6 in Fig. 6E-1) to that with six stamens only two of them bearing two pollen sacs (nodes 6, 12–15 in Fig. 6F-1) in the first-order partial inflorescences; from that with ten stamens five of them with two pollen sacs and others without pollen sacs (node 2 in Fig. 6E-2) to that with six stamens only two of them bearing two pollen sacs (nodes 2 and 9 in Fig. 6F-2) in the second-order partial inflorescences. The degree of development of CL flowers was superior in subtype A than subtype B. CL flowers from the first-order partial inflorescence of subtype A appeared to exhibit a clinal variation in the degree of development from proximal to distal nodes. On the other hand, it was difficult to recognize such clinal variation in the first-order partial inflorescence of subtype B and the second-order ones of both subtypes. The ranges of variation in the numbers of stamens and pollen sacs were continuous between CL flowers of the first- and second-order partial inflorescences like in Type II inflorescences.

The degree of reduction was different between two whorls of stamens like in Type II inflorescences. The stamens lost in CL flowers were all of inner antepetalous ones (2' to 5'), while five outer antesepalous stamens (1 to 5) were retained in all CL flowers in spite of reduction in the number of pollen sacs.

Within the same whorl of stamens, the frequency and degree of reduction were different among the positions of stamens like in Type II inflorescences. In the outer whorl stamens of nos. 3, 4, and 5 were reduced their pollen sacs more frequently and heavily than those of nos. 1 and 2. Even in the most reduced CL flowers, only the stamens of nos. 1 and 2 retained two pollen sacs. In the inner whorl, the reduction was more frequent and obvious in nos. 2', 3', 4', and 5' than in no. 1', and it was most conspicuous in the stamens of nos. 4' and 5'. The stamen of no. 1' was retained in all CL flowers examined, although the pollen sacs were frequently lost.

Discussions

The present study revealed that all of five petals always exist in the CL flower though they are usually reduced to less than 1 mm in size, and that there is variation in degree of reduction of the stamens and pollen sacs in the CL flower. Because the number of stamens per flower and that of pollen sacs per anther vary from ten to six and from four to zero, respectively, the CL flowers represent variations from those with ten stamens each of them

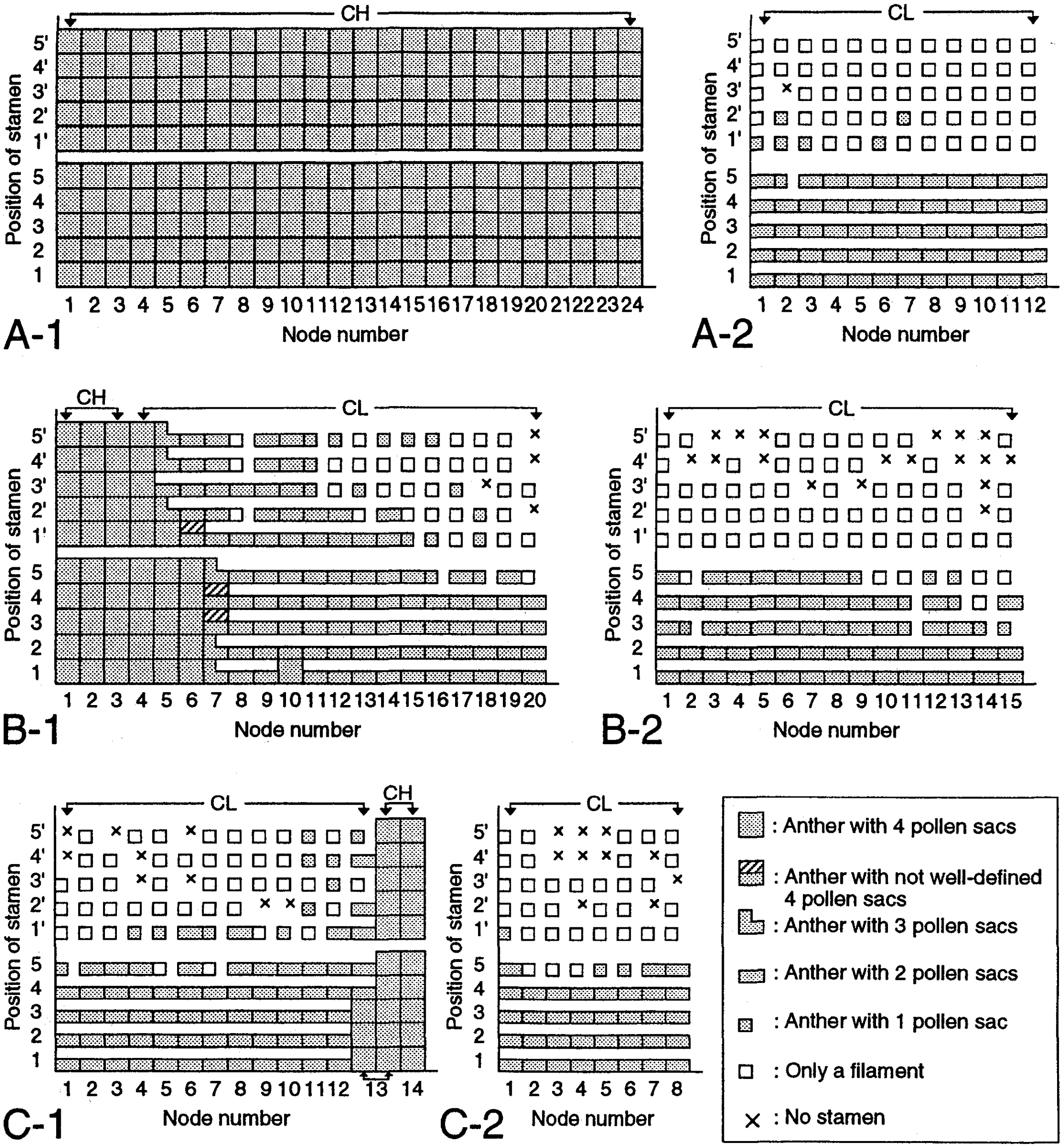

Fig. 6. Variation in numbers of stamens and pollen sacs in relation to the form of inflorescence and the position of flower within one inflorescence. The nodes are numbered from proximal to distal ones. The positions of stamens of 1–5 and 1'–5' within one flower correspond to the positions shown in Fig. 5. A. Inflorescence of Type I. B. Inflorescence of Type IIA. C. Inflorescence of Type IIB. D. Inflorescence of Type IIC. E. Inflorescence of Type IIIA. F. Inflorescence of Type IIIB. A-1, B-1, C-1, D-1, E-1 and F-1 are first-order partial inflorescences, and A-2, B-2, C-2, D-2, E-2 and F-2 are second-order partial inflorescences. In C-1, two flowers were examined from the node of no. 13. CH, CH flower; CL, CL flower. (Material: A, C, D, T. Nemoto 9008301; B, E, T. Nemoto 1392; F, *Takizawa*)

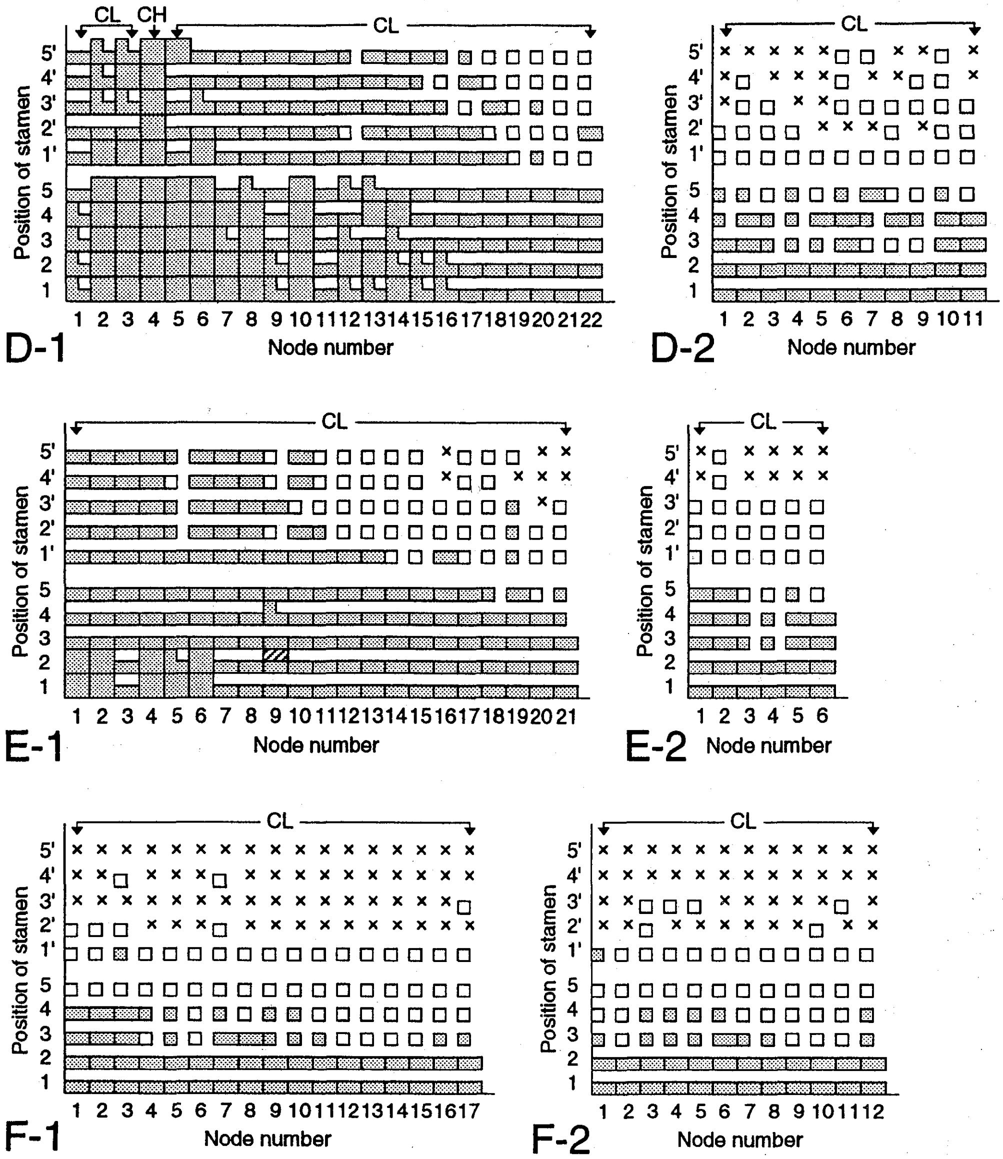

Fig. 6. Continued.

bearing four pollen sacs to those with six stamens two of them bearing two pollen sacs and others without pollen sacs. The CL flower is, therefore, hermaphrodite in spite of the reduction of stamens and pollen sacs in number. Thus, previous recognitions on the CL flowers in *Lespedeza* such as apetalous (Torrey and Gray 1840, Maximowicz 1873, Schindler 1913, Fernald 1950, Blake 1924, Nakai 1927) and unisexual (Torrey and Gray 1840) are inapplicable to *L. tomentosa*. Hanson and Cope (1955), on the other hand, reported that CL flowers are perfect and complete in ten species of *Lespedeza* and they have 5 petals shorter than the calyx and ten anthers. Although they did not examine *L. tomentosa*, their description about anthers is not in perfect agree with the present result, because such complete CL flowers with ten anthers are not common in this species. Truly complete CL flowers which have ten anthers composed of four pollen sacs are borne only at the nodes nearby those producing CH flowers. On the other hand, Blake (1924) mentioned the variation in the degree of reduction of corolla and stamens in CL flowers of American species. American species of *Lespedeza* have been divided into two groups, i.e. species with violet or purple corollas and those with whitish or ochroleucous corollas (Torrey and Gray 1840, Maximowicz 1873, Schindler 1913). According to Blake (1924), the degree of the reduction is different between these two groups and it is greater in the former than the latter. Although *L. tomentosa* has been considered to be more closely related with the latter group (Maximowicz 1873, Schindler 1913), the degree of reduction appears to be more similar to that of the former. However, morphological variation of CL flowers has not yet been examined in detail in American species.

Because CL flowers are obviously modified forms of the CH flowers by reductions in corolla size and the number of stamens and pollen sacs, the cleistogamy in *L. tomentosa* corresponds to Lord's (1981) "true cleistogamy".

In addition, the present study clarified two tendencies in reduction of stamens and pollen sacs: (1) the inner whorl of stamens, or antepetalous stamens, are obliged to be reduced to greater degree and more frequently than the outer one of them, or antesepalous stamens; (2) abaxially located stamens are obliged to be reduced to greater degree and more frequently than adaxially located ones within the same whorl. The most reduced CL flowers have six stamens, two of them are fertile ones with two pollen sacs and others are staminoids without anthers. Five of these six stamens are antesepalous and the rest is antepetalous. Moreover, the fertile stamens are the two antesepalous stamens on the adaxial positions (nos. 1 and 2), and the antepetalous stamen retained is also located at the adaxial position (no. 1'). Similar two tendencies in the reduction of the numbers of stamens and pollen sacs were also reported in *Amphicarpaea bracteata* (as *A. monoica*) by Ritzerow (1908).

Because the anthers are indehiscent and pollen grains are not shedded, pollen grains appear to germinate within the closed anther and elongate their tubes which penetrate the anther wall and then reach the stigma as previously observed in the CL flowers of *Kummerowia stipulacea* (Hanson 1943, 1953, as *Lespedeza stipulacea*). In *L. tomentosa* the most adaxial antesepalous stamens (nos. 1 and 2) are always retained and fertile in the CL flower in spite of reduction in the number of pollen sacs. The style and stigma are strongly curved downward against these stamens, and, therefore, even if the number of stamens decreases, the stigma always has an opportunity to come in contact with at least the anthers of these retained stamens. The collapsed surface of the stigma found after the contact is considered to be induced by a pollen-stigma interaction. Thus, the retention of the most adaxial stamens is closely related to the position of the stigma, and it guarantees self-pollination in spite of reduction of stamens on other positions.

The genus *Kummerowia* with two described species is related to *Lespedeza* (Ohashi et al. 1981; Nemoto et al. 1995), and it has often been treated as congeneric with the latter. Species of this genus also have CL flowers (Schindler 1912, 1913; McKee and Hyland 1941; Hanson 1943, 1953). According to Hanson (1953), the CL flower of *K. stipulacea* has ten stamens each anther of which contains four pollen sacs, although the filaments are free for most of their length and the anthers become smaller in size and contain fewer pollen grains than those of the CH flowers. Thus, the degree of reduction is different between CL flowers of *L. tomentosa* and *K. stipulacea.*

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Endnote

1)The author, (Thunb.), is cited following Bartholomew et al. (Taxon **46**: 311–314, 1977) in the present paper.

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根本智行，大橋広好：マメ科イヌハギにおける閉鎖花の形態変異と花序形態との関連

ハギ属は閉鎖花の有無により2つのグループ，すなわち，閉鎖花をもつメドハギ亜属（subgenus Lespedeza）ともたないヤマハギ亜属（subgenus Macrolespedeza）に分けられている．ハギ属の閉鎖花については，これまで，いろいろに記載されている．1)無弁花である，2)単性である，3)花弁と雄ずいはまったく退化するかそれらの痕跡をもつ，4)閉鎖花には形態の変異があり，ほとんどあるいはまったく花弁が無く雄ずいも非常に退化あるいはまったく欠失するものから花弁をもつものまであらゆる移行段階がある，あるいは5)メドハギ亜属の10種では，閉鎖花が5枚ある花弁のすべてをもち，雄ずいも10本すべてもち，いずれも葯をつける，等である．しかし，従来の記述には相違があり，花弁や雄ずいの有無および退化の程度は明らかではない．また，閉鎖花の形態やその変異については不明な点が多い．そこで，本研究では，ハギ属において分類上重要な形質である閉鎖花について，その形態と変異を明らかにすることにした．閉鎖花の変異を花序内，あるいは花序間で比較するために，メドハギ亜属の中でも，一つの花序あたりの花数が最も多い種のひとつであるイヌハギ *Lespedeza tomentosa* (Thunb.) Siebold ex Maxim.を材料に選んだ．

観察の結果，イヌハギでは花序の形状と閉鎖花形成とが密接に関連していることが明らかになっ

た．花序は葉腋につき，花序主軸基部から第2次花序軸が2本生じ，さらにその基部から第3次花序軸が同様に生じる．第2，第3花序軸には閉鎖花のみが見られたが，花序主軸には開放花のみをつける場合，開放花と閉鎖花をつける場合，閉鎖花のみをつける場合が見られた．そこで，花序主軸の形状を便宜上3タイプ5サブタイプに分け，第1および第1花序軸につく閉鎖花の変異と各花序形態との関連を調べた．

閉鎖花は，すべて，サイズが縮小されているものの5枚ある花弁すべてをつけていた．雄ずいの本数および葯の花粉嚢数では連続的な変異がみられた．すなわち雄ずい本数は10～6本，花粉嚢数は4～0と変異するため，雄ずい10本でおのおのが4花粉嚢をもつ閉鎖花から，雄ずい6本，うち2本だけが2花粉嚢をもつものまでの変異がみられた．花序形態と閉鎖花の雄ずい数および花粉嚢数の変異との関連をみると，第1花序に開放花をつける場合，開放花のつく位置に近付くほど閉鎖花の雄ずい本数と花粉嚢数は増加する傾向がみられた．また，閉鎖花のみをつける場合でも，花序軸や節間が伸長する花序につく閉鎖花は，短縮した花序のものより雄ずい本数と花粉嚢数は増加する傾向がみられた．

また，雄ずいと花粉嚢の退化は，花内での位置と密接に関連することがわかった．花弁と対峙する雄ずい（antepetalous stamens）はがくと対峙する雄ずい（antesepalous stamens）より退化しやすい傾向があり，また，同じ雄ずい群内ではより背軸側に位置する雄ずいが向軸側のものより退化しやすい傾向がある．したがって，本研究で観察された最も退化した閉鎖花は，がくと対峙する雄ずいを5本と花弁と対峙する雄ずいを1本もつ．このうち葯をもつ雄ずいはがくと対峙するものであり，しかも，もっとも向軸側に位置する2本であった．また，1本生じた花弁と対峙する雄ずいも葯は退化しているがやはり最も向軸側に位置する雄ずいであった．閉鎖花では花柱が向軸側に向って湾曲しているため，柱頭はがくと対峙する雄ずいの最も向軸側に位置する2本とのみ接触することができる．閉鎖花では葯が裂開しないため，柱頭と葯との接触によって受粉が起こると考えられる．したがって，雄ずいの退化傾向は，柱頭の位置と密接に関連している．

ハギ属の閉鎖花に関するこれまでの記載は，本研究で明らかになったイヌハギの閉鎖花の形態とは一致しない点が多い．また，ハギ属に近縁と考えられているヤハズソウ属も閉鎖花をつけることが知られている．しかし，雄ずい本数と花粉嚢の退化は起こらないとされており，イヌハギの閉鎖花とは退化の程度が異なる．

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